

PALEOBIOGEOGRAPHIC
DISTRIBUTION OF
KUYLISPORITES AND ITS
POSSIBLE RELATIONSHIP
TO THE EXTANT FERN
GENUS *CNEMIDARIA*
(CYATHEACEAE)¹

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ABSTRACT

The fossil spore genus *Kuylisporites* contains four species, of which *K. mirabilis*, *K. separatus*, and *K. scutatus* seem to be restricted to the Cretaceous and Paleogene of the Northern Hemisphere. The fourth species, *K. waterbolkii*, a spore that has identical features with the spore of the extant fern genus *Cnemidaria*, has been found exclusively in Tertiary to Holocene sediments of the Southern Hemisphere, with a trend to increasing restriction to the Neotropics. *Kuylisporites waterbolkii* has been found in the southern Gondwanan realm from the Early Eocene through early Miocene. New occurrences of *K. waterbolkii*, in middle Eocene sediments from the South Orkney area (Antarctica), link the Paleogene Australian and South American distribution. Between the late Eocene and Oligocene, when dramatic glacial cooling took place, *K. waterbolkii* migrated north. In Australia, where climatic deterioration was balanced by northward drift, *K. waterbolkii* persisted until the early Miocene. Increasing drought in Australia during the Neogene led, however, to its extinction. In South America the distribution area shifted from high latitudes during the Eocene, when climatic conditions there were warm to temperate, to low latitudes during the Oligocene. From the Oligocene on *K. waterbolkii* has been found exclusively in an area that overlaps with the area of extant *Cnemidaria*, which lives mostly in (sub)montane forests in tropical Central/South America and the Antilles. Morphological identity and overlapping paleobiogeographic distribution from the Miocene on suggest that *K. waterbolkii* can be correlated with spores of extant *Cnemidaria*. If this is the case, the Recent area of distribution of *Cnemidaria* must be considered to be a relict area.

Broad austral biogeographic distributions of a large number of plant taxa have been known since work by early botanists such as Hooker in the 1840s (Hooker, 1847). Hooker noticed, for example, that the Falkland Islands, South Georgia, Tristan da Cunha (all in the South Atlantic), and the Kerguelen Islands in the South Indian Ocean, as well as islands south of New Zealand, about 8000 km away from South America, contain plants closely related to taxa from Tierra del Fuego. These observations led botanists, such as, e.g., Engler

(1882), to conclude that Antarctica might have had a bridge function, connecting South America and Australia; these hypotheses were proposed well before modern plate tectonics had explained the fragmentation of Gondwana and subsequent continental movements (Wegener, 1926).

Some plants, including fern, conifer, and angiosperm taxa, are currently distributed on only one of the Southern Hemisphere continents, whereas the paleobotanical record shows a more widespread distribution. Examples of this pattern are the co-

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nifer *Microcachrys* Hook., today restricted to Tasmania but, according to the pollen record, widely distributed in Cretaceous and Tertiary times throughout Gondwana, including Antarctica (Cookson & Pike, 1954).

Antarctica was considered by Copeland (1930) as the possible center of development of many fern families and, in addition, as a bridge between the Gondwanan continents. Even though the idea of Antarctica as an origination center for many ferns is nowadays widely abandoned, the bridge function of this southern continent had been confirmed for certain fern taxa by contemporary palynologists. Askin (1989) was able to show by means of heterochronous stratigraphic occurrences that the Antarctic Peninsula acted as a dispersal corridor in both directions between South America and Australasia for two fern morphs: *Clavifera triplex* Bolkhovitina, a gleicheniacean fern, and *Azolla* spp., a ubiquitous water fern.

Cyatheidites annulatus Cookson ex Potonié is another example of fern migration based on fossil spore data. This fern spore can be correlated with the extant fern genus *Lophosoria* (Dettmann, 1986). *Lophosoria* occurs today throughout much of South and Central America and the Greater Antilles in wet (montane) temperate environments at high altitudes, mostly over 2000 m. Only in southern South America does it also grow at low altitudes. In past geologic times, however, this genus is not known from the tropics, but instead it is known to have occurred in southern high latitudes—in southern South America from the early Cretaceous to the Oligocene, in Antarctica from the early Cretaceous to the middle Eocene, and in Australia and New Zealand until the Pliocene (Dettmann, 1986).

New evidence from *Kuylisporites waterbolkii* Potonié (1956)—a spore identical in appearance to the spores of the extant fern genus *Cnemidaria* Presl (Cyatheaceae)—from sediments of the South Orkney region (Antarctica) adds further credence to the idea that fern taxa have at least occasionally migrated from original high-latitude Southern Hemisphere distributions into lower latitude regions in the Cenozoic.

The high number of *Cnemidaria* species (23 according to Stolze, 1974; plus 2 by Moran, 1990) in northern South America (Colombia and Venezuela), as well as the occurrence there of the most primitive species, led Stolze (1974) to the conclusion that the genus may have originated in this area and migrated to more northerly and southerly sites (Central America and central South America). According to the fossil spore evidence, however,

the genus might have had a more widespread distribution during the Paleogene in the Southern Hemisphere.

The occurrence of *Cnemidaria*-type spores during the early to mid-Middle Eocene in Antarctica can be used as a valuable tool in reconstructing paleobiogeographic distribution patterns and paleoclimatic and environmental conditions during the Cenozoic climatic optimum in southern high latitudes (about 60°S). This climax of Cenozoic warmth is known to have occurred during the time interval of about 58 to 45 Ma. and has been documented in the Weddell Sea and southern Indian Ocean regions by microfossil groups such as foraminifera (Stott & Kennett, 1990; Thomas, 1990) and dinoflagellates (Mao & Mohr, in press; Mohr & Mao, in prep.), and by stable isotope data (Hsü et al., 1984; Kennett & Barker, 1990; Barrera & Huber, 1991).

THE FOSSIL SPORES

The genus *Kuylisporites* contains four species: *K. mirabilis* (Bolkhovitina) Krutzsch, *K. separatus* Chlonova, *K. scutatus* Newman, and *K. waterbolkii*. Excluded from our considerations are the species with a completely different wall structure, which suggest a non-cyatheacean origin. Not considered is, for example, *Kuylisporites lunaris* Cookson & Dettmann, 1958, because it lacks the typical thickenings in the equatorial region and the three well-defined pores, located at the center of the three sides. Dettmann (1963) already stated that *K. lunaris*, found in the Upper Mesozoic of southeastern Australia, differs from all the other known species of *Kuylisporites*.

The oldest species of *Kuylisporites* clearly belonging to the Cyatheaceae is *K. mirabilis*, known from the Cenomanian of Siberia (Bolchovitina, 1953). It also has been reported from the Senonian of the Netherlands and from the Paleogene of Germany (Krutzsch, 1959), where it might have been reworked from Cretaceous sediments (Krutzsch, pers. comm.). Chlonova (1960) found in the Maastrichtian and Paleogene of western Siberia a medium-sized (30–34 μm , average size 32 μm) species of *Kuylisporites*, *K. separatus*, with small rugae on the surface. In this respect, the spore is similar to the North American species *K. scutatus*.

In North America *K. scutatus* existed during the Campanian to Paleocene. It is reported from Colorado (Newman, 1964, 1965), Texas (Evitt, 1973; Beeson, 1992), and New Jersey (Traverse, pers. comm.). This species is very small (average size 27 μm) compared with the (younger) Southern

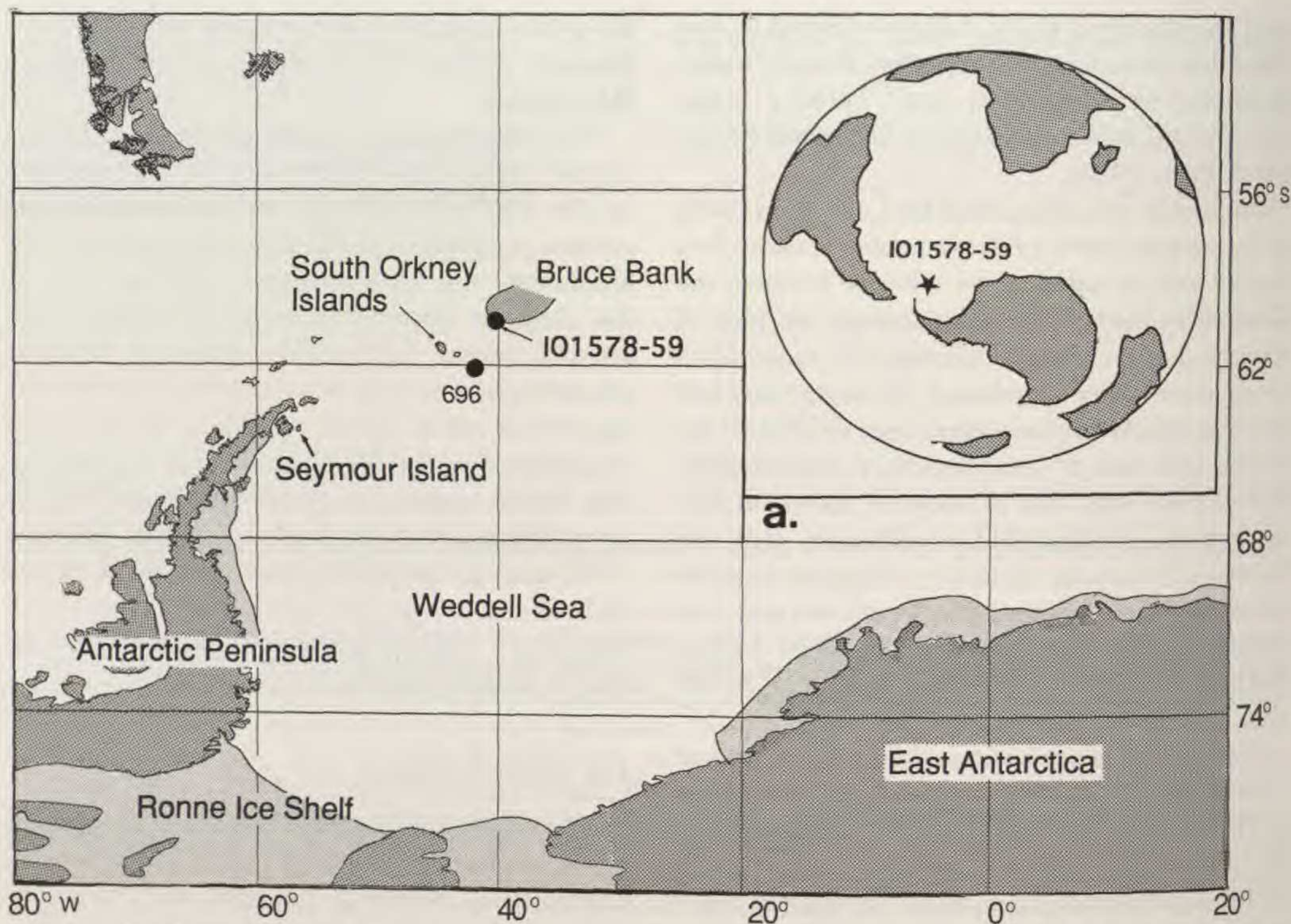


FIGURE 1. Location map of Weddell Sea, Antarctica showing location of Florida State piston core Islas Orcadas (IO) 1578-59, Ocean Drilling Program Site 696, and other geographic features referred to in the text. Light stipple pattern along edge of Antarctic continent indicates ice-shelf. Inset (a) shows approximate location of core IO1578-59 in middle Eocene times. Continental reconstruction created using Terra Mobilis program of Denham & Scotese (1987).

Hemisphere species *K. waterbolkii* and has, according to the original description, a slightly rugulate surface on the distal side (Newman, 1965). Furthermore, this species lacks any additional scattered pores.

Kuylisporites waterbolkii is known from the late Early Eocene on from southeastern Australia (Stover & Partridge, 1973). *Kuylisporites waterbolkii*, often named *Hemitelia* by various authors (see below), has been observed in Central and South America from the Oligocene on.

A list of the known fossil occurrences of the spore genus *Kuylisporites* is given in an Appendix to this paper.

SPORES FROM BRUCE BANK, OFF THE NORTHERN ANTARCTIC PENINSULA

a. Material and method

New evidence has been found from middle Eocene (43–50 Ma.) marine strata from the South Orkney area (Fig. 1). The material was collected during the Islas Orcadas cruise 1578 (Cassidy,

1980), at Bruce Bank, South Scotia Ridge off the northern Antarctic Peninsula (Latitude 60°33'S; Longitude 40°13'W; mbsl: 2707 m, see Fig. 1). According to Toker et al. (1991), the nannofossil assemblage found in these strata can be assigned to the *Chiasmolithus gigas* Subzone of the *Nannotetrina quadrata* Zone, which equals late early to mid Middle Eocene. Following Berggren et al.'s (1985) timescale, an absolute age of about 47 to 49 Ma. (see Bolli et al., 1985) can be estimated.

The material for this study comes from the upper 130 cm of a 3.85-m-long piston core (IO1578-59), which contains olive gray to olive brown compacted clay. From this interval six samples were taken, which were processed using standard centrifuge preparation techniques. In addition, sieving with a 15 μ m sieve and oxidation with HNO₃ were also carried out. The latter procedure was necessary because of the high amount of pyrite that filled a good part of the palynomorphs. From every sample four smear slides mounted with glycerine jelly were prepared.

The material is rich in well-preserved dinofla-

gellate cysts (Mao & Mohr, in press), fungal and fern spores, and gymnosperm and angiosperm pollen (Mohr, in prep.).

From Core IO1578-59 more than 30 different spore taxa were identified, with an average diversity of about 15 to 20 taxa per sample (Mohr, in prep.). Most of these spore taxa can be assigned to ferns; a few genera, however, have been derived from mosses and lycopods. *Cnemidaria*-type spores occur regularly, but with a frequency of only about 2 to 4 specimens per slide, equaling about 0.5% to 1.0% of the total sporomorph content.

b. Description of Cnemidaria-type spores from the South Orkney area

Kuylisporites waterbolkii Potonié (1956), Figure 2A, B, C.

Trilete spores, amb rounded triangular. Laesurae unthickened, straight, long (up to $\frac{1}{5}$ of the total spore diameter). Foveolate, small foveae (1–5 μm) scattered irregularly over the entire spore surface. Three large pits (diameter about 5–7 μm) are found symmetrically arranged at the center of the three sides. There, the thickness of the two-layered wall is usually increased (from 1.5 to 3 μm). Size of the spores: 27–(32)–35 μm .

Comments: In size somewhat smaller than spores of most extant species of *Cnemidaria*, but otherwise identical.

GEOGRAPHY AND ECOLOGY OF EXTANT *CNEMIDARIA*

The geographic range of living *Cnemidaria* with its 25 species (Moran, 1990) covers the area of Central America, the Greater Antilles, and the northern part of South America (Tryon & Tryon, 1982). The distribution is generally continuous, with species overlapping through most of the range (Stolze, 1974). There are however, according to this author, two notable regions of disjunction: southeastern Brazil, and an area containing the Mexican provinces of Chiapas and Oaxaca and the Guatemaltecan province of Alta Verapaz.

Most *Cnemidaria* species have a subarborescent habit, with leaves usually less than 1 m in length. These ferns are largely confined to deeply shaded, moist habitats, in or at the edges of forests, sometimes along creeks and waterfalls, at elevations ranging from sea level to 2300 m, but typically between 500 and 2000 m (Stolze, 1974). Lellinger (1975) reported *Cnemidaria* from Colombia (Dep. del Chocó), where it was mostly seen at roadsides at altitudes at or below 500 m, rarely up to 1000 m. Mägdefrau (1960) gave more precise data for

one of the areas of occurrence of *Cnemidaria*, in the cloud forests of the "Rancho Grande" in northern Venezuela. There, the cloud forest is found at altitudes between 1150 m and about 2350 m. The annual precipitation is about 1750 mm, with most of the precipitation (1600 mm) falling during the season from April through November. Daily temperature ranges are generally low (16–21°C).

THE SPORES OF EXTANT *CNEMIDARIA*

Many features of the extant genus *Cnemidaria* are partially shared with other cyatheacean genera (Stolze, 1974; Tryon & Tryon, 1982), but trilete spores with three large pits are unique to this fern genus. *Cnemidaria* spores are characterized by three pores in the equatorial area, equidistant between the laesurae and often with additional smaller pores (Fig. 2). In fact, this spore type is graphically so special that the Laboratory of Palynology of the University of Amsterdam (Hugo de Vries-Laboratorium) chose the outline of this taxon as its logo.

Spores of extant *Cnemidaria* were previously described in detail by Erdtman & Sorsa (1971) and by Stolze (1974), and were well documented by Tryon & Lugardon (1991). According to Stolze (1974) the approximate lateral diameter is 37 to 52 μm . The surface of the exospore is more or less smooth, but shows three typical large pores (up to 15 μm diam.), located at the center of each of the three sides. Additional pores of different size may be distributed randomly over the spore surface.

We have examined spores from the following extant species: *C. choricarpa* (Maxon) Tryon, Costa Rica, Pittier & Durand 4835; *C. cocleana* Stolze, Panama, Franco 14880; *C. horrida* (L.) Presl, Venezuela, A. Smith 948; *C. mutica* (Christ) Tryon, Costa Rica, Hennipman 6739; *C. roraimensis* (Domin) Tryon, Guyana, Pipoly 10789; *C. spectabilis* (Kunze) Tryon, French Guyana, Cremers 10172.

We confirm the spore morphology descriptions cited above, with one addition: In very rare cases some of the spores show more than three main pores (Fig. 2G). This is also true for fossil material (Fig. 2C).

We show in this paper that the paleobiogeographic distribution pattern of *Kuylisporites waterbolkii* spores fits with the idea that *K. waterbolkii* is a spore belonging to an ancestral or closely related form of *Cnemidaria*. These ancestral species might have been a species of *Cyathea*, since many of the spores of *Cyathea* have a pitted exo-

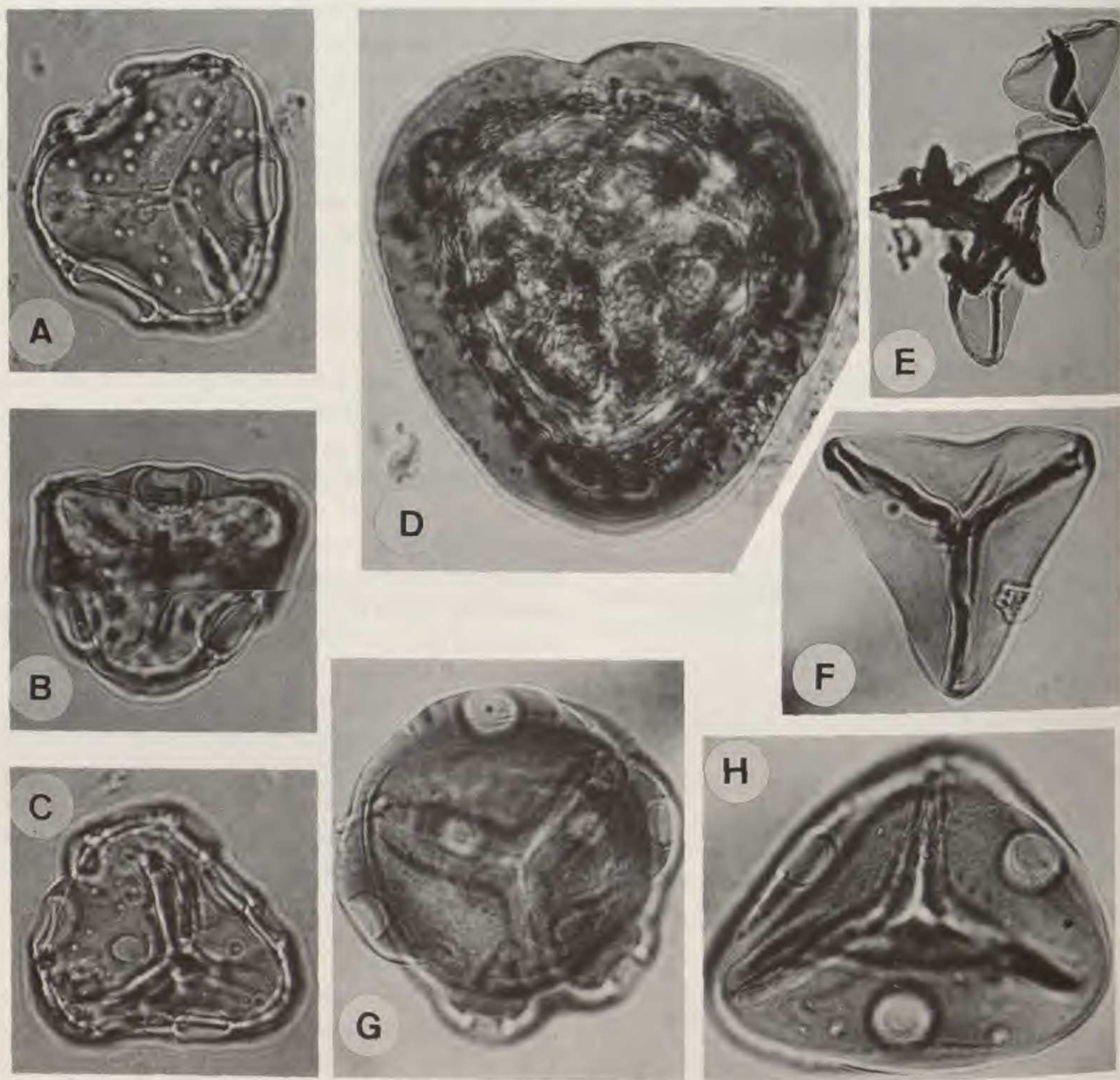


FIGURE 2. A. *Kuylisporites waterbolkii*; Sample 1578-59, 26-28 cm; Slide B, $\times 1000$.—B. *Kuylisporites waterbolkii*; Sample 1578-59, 123-125 cm, Slide D, $\times 1000$.—C. *Kuylisporites waterbolkii*; Sample 1578-59, 26-28 cm; Slide B, $\times 1000$.—D. *Cyatheacidites annulatus*; Sample 1578-59, 123-125 cm; Slide A, $\times 1000$.—E. *Alsophila decurrens* var. *decurrens* Hook., Upolu (Samoa), Sledge 1523, $\times 250$.—F. *Alsophila decurrens* var. *decurrens* Hook., Upolu (Samoa), Sledge 1523, $\times 1000$.—G, H. *Cnemidaria horrida* (L.) Presl, Venezuela, A. Smith 948, $\times 1000$.

spore. However, these pits are irregularly distributed and vary in size and are often obscured by a perispore. The similarity of the two spore-types is not surprising, because *Cyathea* and *Cnemidaria* are closely related. In fact, they are considered by some authors as subgenera (Kramer & Green, 1990) because of the presence of "intergeneric" hybrids (Holttum & Edwards, 1983).

PALEOBIOGEOGRAPHIC PATTERNS

The reported occurrences of species of *Kuylisporites* spores can be used to infer the paleobiogeographic history of this group. Equally important, however, is information on where they have

not been found, since without such negative evidence, we cannot map the limits of its past distribution. Arguments based partly on negative evidence may be risky, as future discoveries may change an area of non-occurrence to one of occurrence. We have tried to minimize this possibility by considering *Kuylisporites* to be absent from a region only when there are well studied floras from the region. Based on this reasoning, a summary of the past geographic distribution of *Kuylisporites* is given in Table 1 and Figure 3. Table 1 is based on our knowledge of the palynological literature, although for reasons of space, we give and discuss citations only for cases of occurrence of *Kuylisporites*.

TABLE 1. Distribution of *Kuylisporites waterbolkii* (X) and *Kuylisporites* sp. (+) spores by geologic age and geographic area. Also shown is distribution of known floras which lack *Kuylisporites* (□). Dashes in Antarctica column indicate interval with no records due to continental glaciation.

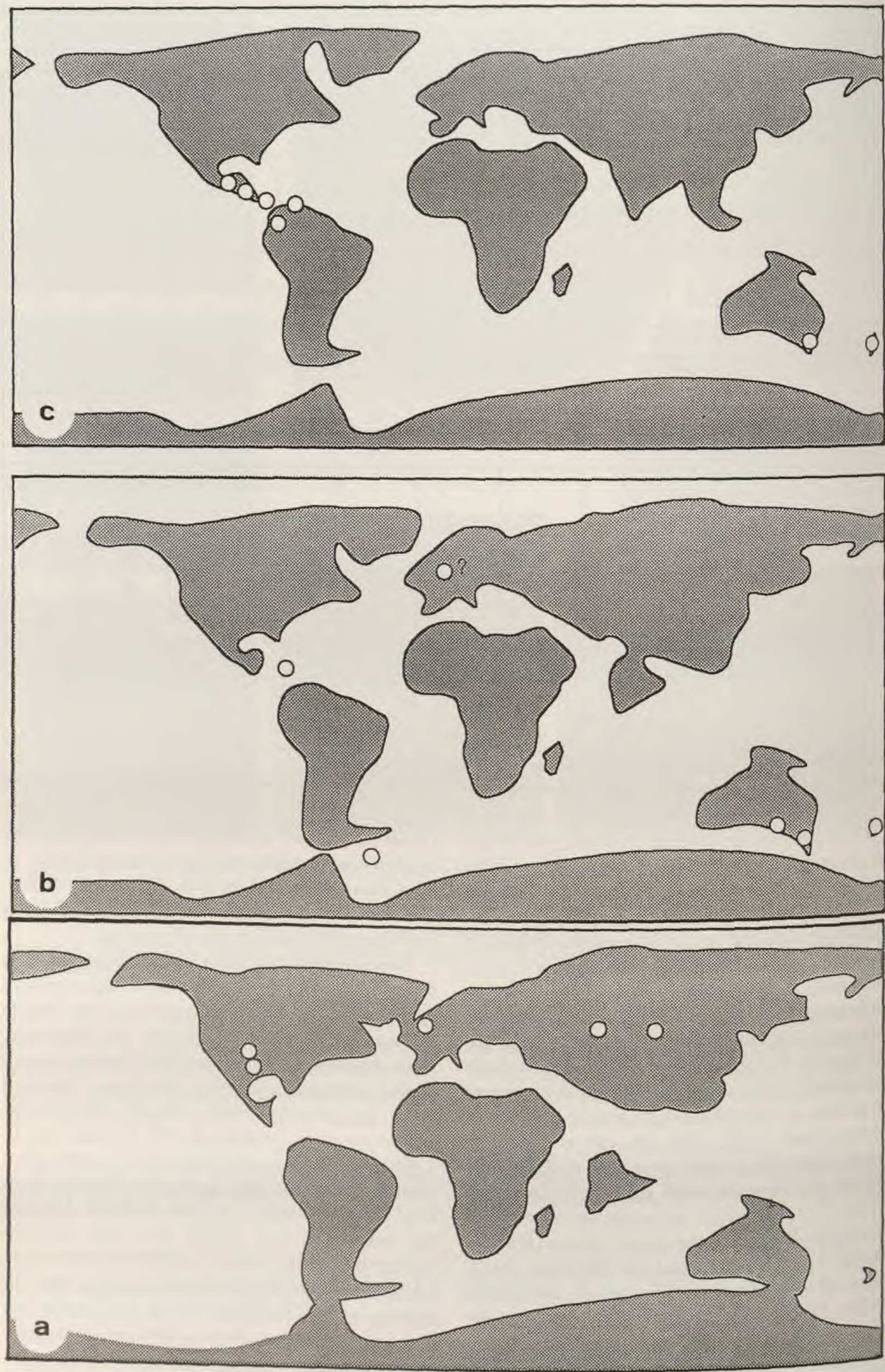
		Asia	Europe	North America	Central America	South America	Antarctica	Australia	New Zealand
Recent		□	□	□	×	×	—	□	□
Quaternary		□	□	□		×	—	□	□
Pliocene		□	□	□	×	×	—	□	□
Miocene	L								
	M	□	□	□	×		—	□	
	E				×			×	×
Oligocene	L							×	×
	E	□	□	□	×		□	×	
Eocene	L							×	
	M		+				×	×	×
	E							×	
Paleocene		+		+			□	□	□
Maastrichtian		+	+	+			□		
Pre-Maastr.		+	+	+			□		

Pre-Paleogene occurrences of *Kuylisporites* are known only from the Northern Hemisphere (Table 1, Fig. 3a). These spores, even though they resemble *K. waterbolkii* in their general aspect, are sufficiently different as to be considered directly ancestral or related to the genus *Cnemidaria*, i.e., most likely of cyatheaceous origin but not necessarily identical to *Cnemidaria*. True *Cnemidaria*-type spores (*K. waterbolkii*) are found from the mid-Eocene on exclusively in the most southerly palaeofloral province, the *Nothofagidites* province recognized in Australia, South America, and Antarctica (Table 1, Fig. 3b). The oldest strata containing *Cnemidaria*-type spores are of (late) early Eocene age from Australia (Stover & Partridge, 1973). The next oldest occurrences are those of the middle Eocene of the South Orkney Plateau, described in this paper, and the Oligocene occurrences of New Zealand (Pocknall & Mildenhall, 1984). The genus is not reported earlier than the Oligocene from the Caribbean (Puerto Rico).

Neogene occurrences of *Cnemidaria*-type spores

(Table 1, Fig. 3c) are restricted to early Miocene localities in Australia and New Zealand (Stover & Partridge, 1973; Pocknall & Mildenhall, 1984), and several locations in the Caribbean, Central America, and northern South America.

This distribution pattern can be interpreted as follows: *Cnemidaria* sp. occurred at high southern latitudes from the Early Eocene through the Middle Eocene. Between the late Eocene and Oligocene, when dramatic cooling took place, caused by successive Antarctic glaciation, the genus migrated north. In Australia, where climatic deterioration was balanced by northward drift (Veevers et al., 1990), *Cnemidaria* persisted until the early Miocene. Increasing drought during the Neogene, however, led to its extinction there. In South America the distribution area shifted from high latitudes during the Eocene, when climatic conditions were warm-temperate, to low latitudes during the Oligocene, where *Cnemidaria* lived, and mostly still lives, in (sub)montane forests under tropical to temperate conditions. Only a few species, such as *C.*



spectabilis, are also occasionally found in the low-land forests of northern South America (Kramer, pers. comm.).

Kuylisporites has not been reported from South Africa (Coetzee et al., 1983, and literature cited there). The separation of South Africa from South America and Antarctica began as early as the late Jurassic. Antarctica had drifted far south by the early Cretaceous. The non-existence of *Cnemidaria* in South Africa is a strong hint that the genus must have spread over the Southern Hemisphere after Antarctica had drifted away from Africa—that is, not earlier than in the late Cretaceous.

Finally, the Quaternary distribution in Table 1 sheds light on the possibility that *Cnemidaria*-type spores are present in other living species of Cyatheaceae, as not all have as yet been closely examined. Table 1 suggests that only those species which are today restricted to Central America and northern South America might possess such spores, as spores of this type are not reported from Quaternary to sub-Recent sediments elsewhere.

There is one exception to this argument. One other member of the genus *Alsophila* (Cyatheaceae), *Alsophila decurrens* var. *epaleata* Holttum, found on the Society Islands (Polynesia), exhibits similar wall structures (Tryon & Lugardon, 1991). We examined material in the collections of the Botanical Garden of Zürich (*Alsophila* (Cyathea) *decurrens* Hooker, Sledge 1523, Upolu, Samoa) and plates already published in the literature (Gastony & Tryon, 1976: 574). In addition, copies of SEM photographs, generously given by A. F. Tryon from *Alsophila decurrens* var. *epaleata* (collection of Grant 5231, Society Islands), were used for our studies. We note that in *A. decurrens* var. *decurrens* (Fig. 2E, F) the exospore seems to be smooth under the light microscope. Only SEM pictures reveal the microreticulate surface of the exospore (Gastony & Tryon, 1976). The 3-pitted spore type seems to occur only in *A. decurrens* var. *epaleata*. In *Cnemidaria*, the distinctive 3-pitted structures are uniformly developed, showing very little variation in morphology. In contrast, *A. decurrens* var. *epaleata* seems to have a relatively broad range of pore size ranging from big pores, like those seen in spores of *Cnemidaria*, to relatively small pores,

not much bigger than those encountered in *A. decurrens* var. *decurrens*. In addition, Gastony & Tryon (1976) noted that in contrast to *Cnemidaria*, all the varieties of *Alsophila decurrens* seem to develop in the mature stage a perine layer around the exine. This fact and the range of morphologic variability, quite unlike *Cnemidaria*, suggest that the 3-pitted forms occasionally seen in *Alsophila* are only coincidentally similar to *Cnemidaria*, and are not truly homologous. Although the origin of pored spores in this species is of some evolutionary interest, the occurrence of 3-pitted spores in *Alsophila* does not appear to be directly related to the biogeographic history of *Cnemidaria* spores discussed in this paper.

We therefore conclude that the association of this distinctive spore's distribution in Quaternary sediments with the one widespread extant taxon known to possess this spore (*Cnemidaria*) supports the use of *Cnemidaria*-type spores as a tracer for the genus.

CONCLUSIONS

1. The cyatheaceous spore genus *Kuylisporites*, comprising four species, originated in the Northern Hemisphere in the late Cretaceous.

2. *Kuylisporites waterbolkii*, closely related to or identical with extant *Cnemidaria*, is known from the Early Eocene on. It was restricted to the Southern Hemisphere realm, where it shows a typical disjunct distribution, being absent from Africa. From the Middle Miocene on the biogeographic distribution of *K. waterbolkii* becomes gradually restricted to the area where *Cnemidaria* occurs today. Therefore, Central and South America and the Antilles might be considered a relict area for this genus.

3. Some fern taxa associated with *K. waterbolkii*, such as *Cyatheacidites annulatus* (Lophosoria, Lophosoriaceae), confirm the ecological interpretation of *K. waterbolkii* as an indicator of warm-temperate, not fully tropical climate. To remain in the same warm-temperate environment in which the *K. waterbolkii*-producing fern grew in southern high latitudes during the Paleogene, *Cnemidaria* migrated north when Antarctica became heavily glaciated during the Oligocene. Since

FIGURE 3. Location of *Cnemidaria* and *Cnemidaria*-like spores (o) on paleogeographic reconstructions created using Terra Mobilis program of Denham & Scotese (1987).—a. Cretaceous–Paleocene occurrences on a 68 Ma. map.—b. Eocene–Oligocene occurrences on a 45 Ma. map.—c. Neogene occurrences on a 15 Ma. map. More detailed information on localities is given in Table 1 and the Appendix.

most of the species of *Cnemidaria* seem to avoid fully tropical lowland habitats, *Cnemidaria* migrated in South America to higher elevations during the Neogene.

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- APPENDIX. Occurrences and publications of *Kuylisporites* sp.
- 1953 *Hemitelia mirabilis* Bolkhovitina: Bolkhovitina (1953: 47, pl. 6, fig. 10); Cenomanian of USSR, eastern slope of the South-Ural, near Nowo-Nikolaewskogo.
- 1955 Cyatheaceae (*Hemitelia* type): Kuyli, Muller & Waterbolk (1955: pl. 1, fig. 7); late Tertiary of Trinidad.
- 1956 *Kuylisporites waterbolkii* Potonié: Potonié (1956: 103, pl. 4, fig. 39).
- 1959 *Kuylisporites mirabilis* (Bolkhovitina) Krutzsch: Krutzsch (1959: 190), based on *Hemitelia mirabilis*, published by Bolkhovitina in 1953.
- 1960 *Kuylisporites separatus* Chlonova: Chlonova (1960: 11, pl. 1, figs. 6 and 7); Maastrichtian and Paleocene of western Siberia.
- 1960 *Hemitelia*: van der Hammen & Gonzalez (1960: 296, pl. 16, fig. 126); Quaternary of Colombia, perhaps reworked.
- 1961 *Kuylisporites* (cf. *Hemitelia*) sp.: Samoilovitch et al. (1961: pl. 79, fig. 4); Maastrichtian of the USSR (citation from Dettmann, 1963).
- 1964 *Kuylisporites* sp.: Newman (1964: 174, pl. 1, fig. 4); late Cretaceous of Colorado.
- 1965 *Kuylisporites scutatus* Newman: Newman (1965: 9, pl. 1, fig. 1); Campanian of northwestern Colorado.
- 1969 *Hemitelia* (*Cnemidaria*): Graham & Jarzen (1969: 317, fig. 9); Oligocene of Puerto Rico.
- 1973 *Kuylisporites scutatus* Newman: Evitt (1973: 33, pl. 1, fig. 19); Maastrichtian and Paleocene of Texas.
- 1973 *Kuylisporites waterbolkii* Potonié: Stover & Evans (1973: pl. 3, fig. 13); late early Eocene to late Eocene off southeastern Australia.
- 1973 *Kuylisporites waterbolkii* Potonié: Stover & Partridge (1973: 249); early Eocene to early Miocene of southeastern Australia.
- 1976 *Hemitelia*: Graham (1976: 812, figs. 23, 24); Miocene of Mexico.
- 1984 *Kuylisporites waterbolkii* Potonié: Pocknall & Mildenhall (1984: 20 pl. 2, fig. 6); late Oligocene to early Miocene of New Zealand.
- 1988 *Cnemidaria*: Graham (1988: 10, 11); early Miocene of Costa Rica.
- 1989 *Kuylisporites waterbolkii* Potonié: Macphail & Truswell (1989: 330); late Eocene to early late Oligocene, Murray Basin, southeastern Australia.
- 1991 *Cnemidaria*: Graham (1991: 193, 194, figs. 12, 13); Pliocene of Panama.
- 1994 *Kuylisporites waterbolkii* Potonié: Mohr & Lazarus (1994, this paper); mid-Eocene, Bruce Bank, South Orkney area.